PRECOPULATORY BEHAVIOR OF THE WHIRLIGIG BEETLE DINEUTES DISCOLOR (COLEOPTERA:GYRINIDAE)

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Abstract.—The sexual behavior of whirligig beetles is more complex than has previously been described. Precopulatory mounting is a behavior pattern performed by males, and proleg-up is performed by females. These interactions are more in accord with the potential complexities of mate selection and sexual synchronization than earlier accounts of whirligig courtship behavior.

Precopulatory communication is believed to be important in allowing animals to select mates of the appropriate species and of robust phenotype, and in synchronization of sexual behavior. It is of special interest therefore, when the accounts of a species' reproductive behavior seems to preclude any interactions complex enough to facilitate these processes. The only descriptions of whirligig beetle precopulatory behavior speak of males merely leaping on females and inseminating them (Smith, 1926), which in light of current ideas about sexual communication seems unlikely. I undertook this study in order to uncover any behavior interactions in gyrinid precopulatory behavior that might supply a context in which precopulatory communication of a more substantial sort might occur.

These beetles have four compound eyes, have good vision (Bennett, 1967; Carthy and Goodman, 1964) and appear to be very visually oriented (Brown and Hatch, 1929). As surface film dwelling predators, whirligigs have evolved antennal specializations that allow their Johnston's organs to serve as extremely sensitive surface vibration detectors (Wilde, 1941; Rudolph, 1967). Other analogous surface vibration detectors occur in insects found at the air-water interface (Murphey, 1971, 1973; Murphey and Mendenhall, 1973) and in some cases precopulatory signals are transmitted via surface film vibrations (Wilcox, 1972, 1979).

The basic gyrinid body plan consists of streamlined elytra covering the thorax and abdomen, with flat paddle-like mesothoracic and metathoracic legs that are efficient swimming organs (Nachtigall, 1961). The long, slender

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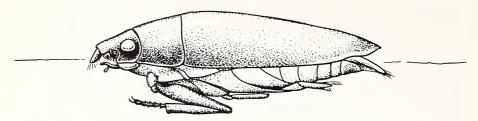


Fig. 1. A view of *Dineutes discolor* swimming. The prothoracic leg is shown lowered somewhat so that its form is apparent.

prothoracic legs are used to seize prey and are held under the beetles' bodies in recessed grooves when unused (Fig. 1 shows these legs lowered somewhat).

MATERIALS AND METHODS

Dineutes discolor were removed from a swarm located on the Wisconsin River near Arena (Iowa Co.), Wisconsin in September 1977 and throughout May and June 1978. The beetles were housed in screen-covered aquaria filled with tap water and fed live flightless *Drosophila*. Approximately 70 beetles individually marked on their elytra with Testor's PLA enamel paints were used in my observations.

The observation tank was a $92.5 \times 46.5 \times 46.5$ cm aquarium containing floating vegetation and live prey. The beetles were therefore free to climb out of the water or feed, rather than being constrained to interacting in a more impoverished environment. Observations were normally for 55 min sessions, occasionally 44 min.

The rates at which every pair of beetles performed different behavior patterns were recorded and Mann-Whitney U tests (Siegel, 1956) were used to compare the behavior patterns performed by beetles which mated to the data collected during observation periods during which the beetles did not mate. It is important to note that all data from subjects that were never observed to mate were discarded, so that nonmating data were collected

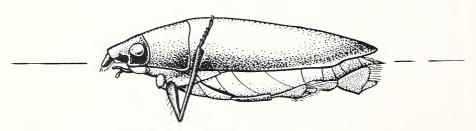


Fig. 2. A proleg-up performed by a female beetle.

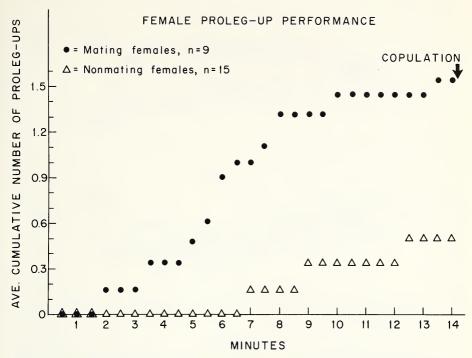


Fig. 3. Performance of the proleg-up behavior by female beetles, in observations with one pair of beetles present. Values for control females are based on the first 14 min of each observation of nonmating pairs (which was the average precopulatory interval in mating pairs).

from animals known to be capable of carrying out successful precopulatory sequences at other times.

RESULTS

I conducted 56 observation periods, during which 24 copulations were observed. Twenty-four observation periods had one pair of beetles present in the experimental apparatus, and 32 of the observations had two pairs present. Data collected in these two situations were consistent with one another in form and in statistical significance, and they are reported together. Data on fifteen behavior patterns were collected. These categories included: different postures of legs and elytra, mouthpart movements, proximity and contacts between beetles, diving, swimming, climbing, general activity level, feeding, and grooming. Of these behavior patterns, only two proved to be statistically related to successful copulation.

Female beetles perform a behavior pattern called *proleg-up* more frequently before they copulate (Mann-Whitney U test, P < 0.05). This act

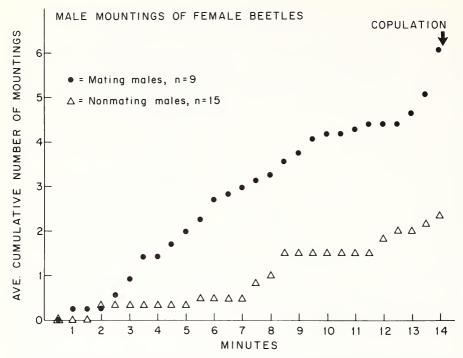


Fig. 4. Male mountings of female beetles, in observations with one pair of beetles present. Values for control males are based on the first 14 min of each observation of nonmating pairs (which was the average precopulatory interval in mating pairs).

consists of the beetle swinging her leg out toward the lateral margin of her body, flexing the leg so that its distal region (tibia and tarsus) extends perpendicularly up from the water, and then rapidly reversing these movements (Fig. 2). Male performance of proleg-up is not statistically related to ensuing copulation.

The data in Figure 3 show the average number of proleg-up performances plotted against time to copulation, for female beetles observed with one male present. The proleg-up behavior has reached almost its final level when copulation is still 5 min away. It appears therefore to be a signal used early in precopulatory communication, rather than in the final stages. No specific distance or direction between male and female during proleg-up performance was noted, but this may have been an artifact of their relatively enforced proximity in the observation aquarium.

Male beetles *mount* female beetles more frequently before they copulate (Mann-Whitney U test, P < 0.05), with the males clinging to the dorsal surface of the females for periods ranging from very brief to 10 min. These mounts do not involve insertion of the male genitalia (those were scored

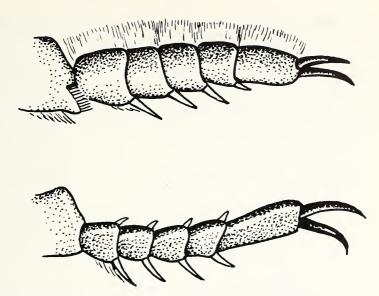


Fig. 5. Male (above) and female (below) tarsal segments of the prothoracic leg.

separately as copulations). Interestingly although male/male, male/female, and female/male mounts were all common, only male/female mounts are especially associated with successful precopulatory sequences.

The data in Figure 4 show the average number of male mountings of females, plotted as in Figure 3. These mountings continue throughout the precopulatory exchange, increasing in rate somewhat in the final 2 min before copulation. Beetles are adjacent to one another immediately before a mounting, but no specific direction of approach by the male relative to the female was apparent.

DISCUSSION

Based on statistical analysis of rates of different precopulatory behavior patterns, mountings of females by males and proleg-up by females may be serving in the precopulatory communication of *Dineutes discolor*.

The proleg-up behavior pattern exposes the distal segment of the prothoracic leg as high above the water line as is possible. This leg region is the animal's one strikingly sexually dimorphic characteristic (Fig. 5) aside from the form of the genitalia themselves. This behavior pattern may therefore serve to demonstrate sexual identity and indicate willingness to copulate.

The occurrence of males mounting females as a precopulatory display is known in a wide variety of animal species. These mountings in *D. discolor* are best viewed as signals rather than as unsuccessful attempts to copulate,

especially in light of the facts that (a) females mount males, (b) males mount other males and (c) the male genitalia are not extended during any of these mountings.

The sensory channels that might be involved in the proposed displays of *D. discolor* are diverse, but visual transmission seems likely for the prolegup and tactile transmission seems likely for male/female mountings. In the latter, ample tactile cues are certainly present—although contact chemoreception cannot be ruled out. In the former, the striking sexual dimorphism of the distal prothoracic leg segments could be easily apparent via visual cues—but again, due to the remarkable sensitivity of the gyrinid surface vibration detector (Rudolph, 1967) a second stimulus channel cannot be ruled out.

The proleg-up performance by female beetles reaches a plateau early in precopulatory exchanges, and is more likely to be involved in initially signalling for female receptivity than in facilitating the final approach of the male for copulation. Male mountings of females occur throughout the precopulatory period, and increase somewhat in frequency during the last 2 min before copulation. This behavior may be involved both in signalling sexual readiness, and in facilitating the final synchronization and orientation of the beetles for copulation.

This type of observational study is inherently limited in its conclusion. In order to further elucidate the signal value of these behavior patterns, either their performance or perception would have to be experimentally manipulated and the results observed. Nonetheless, this study is adequate to strongly indicate that whirligig precopulatory behavior contains interactions that could supply the reciprocal complexity we have come to expect in situations where mate selection or sexual synchronization occur.

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LITERATURE CITED

- Bennett, R. R. 1967. Spectral sensitivity studies on the whirligig beetle, *Dineutes ciliatus*. J. Insect. Physiol. 13:621–633.
- Brown, C. R. and M. H. Hatch. 1929. Orientation and "fright" reactions of whirligig beetles (Gyrinidae). J. Comp. Psychol. 9:159-189.
- Carthy, J. D. and L. J. Goodman. 1964. An electrophysiological investigation of the divided eye of *Gyrinus bicolor*. J. Insect Physiol. 10:431–436.

- Murphey, R. K. 1971. Sensory aspects of the control of orientation to prey by the waterstrider, *Gerris remigis.* Z. Verg. Physiol. 72:168–185.
- Murphey, R. K. 1973. Mutual inhibition and the organization of a non-visual orientation in Notonecta. J. Comp. Physiol. 84:31–40.
- Murphey, R. K. and B. Mendenhall. 1973. Localization of receptors controlling orientation to prey by the Back Swimmer *Notonecta undulata*. J. Comp. Physiol. 84:19–30.
- Nachtigall, W. 1961. Funktionelle Morphologie, Kinematik, und Hydromechanik des Ruderapparates von *Gyrinus*. Z. Vergl. Physiol. 45:193–226.
- Rudolph, P. 1967. Zum ortungsverfahren von Gyrinus substriatus (Steph). Z. Vergl. Physiol. 56:341–375.
- Siegel, S. 1956. Nonparametric Statistics for the Behavioral Sciences. McGraw Hill Book Company, New York.
- Smith, H. B. 1926. Notes on the behavior of *Dineutes americanus*. Psyche 33:156-161.
- Wilcox, R. S. 1972. Communication by surface waves in the mating behavior of a water strider (Gerridae). J. Comp. Physiol. 80:255-266.
- Wilcox, R. S. 1979. Sex discrimination in *Gerris remigis*: role of a surface wave signal. Science 206:1325–1327.
- Wilde, J. de 1941. Contribution to the physiology of the Johnston organ and its part in the behavior of the Gyrinus. Arch. Neer. Physiol. Homme Animaux 25:381–400.

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